Limnologica **31** (2001) 119–128
http://www.urbanfischer.de/journals/limno

LIMNOLOGICA

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Assessing Small-scale Directional Movements of Benthic Invertebrates in Streams by Using a Multidirectional Cage Trap

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With 5 Figures and 3 Tables

Key words: Directional movement, MDC-Trap, modular sampling design, taxon-specific movement patterns, colonization activity

Abstract

A multidirectional cage trap (MDC-Trap) was developed in order to assess small-scale directional movements of benthic invertebrates in streams. The trap can be operated with causing minimal disturbance to the stream bed and enables repeated sampling of identical patches of stream bottom. The MDC-Trap combines characteristics of net samplers with features of colonization-substrate samplers. It is made out of a perforated plywood box which is divided into nine compartments. Each compartment is loaded with a gravel-filled directional cage that can be colonized from one direction only. The modular design of the MDC-Trap allows assessing of up to nine different types of invertebrate movement simultaneously: upstream, downstream and lateral on the substrate surface as well as subsurface movements upstream, downstream and lateral. If necessary, distinctions can be made between left and right oriented movements. Furthermore, movements vertically upward from within the hyporheos can be recorded. The MDC-Trap was designed to be used in streams with coarse sand, gravel or pebble substrates. The device is constructed so that there is no clogging and, once exposed, the trap can be left in the stream indefinitely. The results of first field tests show that the MDC-Trap is suitable to characterize small-scale movements of invertebrates in gravel streams. Net longitudinal movement was in the downstream direction for most species, although the taxon-specific patterns varied considerably. In particular, *Baetis rhodani* and *Hydropsyche* spp. exhibited a clear preference for downstream movement by drifting or crawling and seldom displayed upstream or lateral movement. Preference for downstream movement was less pronounced for chironomids, *Eucyclops serrulatus* and *Gammarus pulex*. Other taxa were about equally distributed among the direction-sensitive subunits. No taxon exhibited large-scale upstream movement. These findings are in contrast to the idea of compensatory migrations.

Introduction

Small-scale movements of benthic invertebrates are an important basis for the spatial microdistribution pattern of the lotic community. Continuous redistribution (TOWNSEND & HILDREW 1976) leads to a flux of individuals among microhabitat patches. Small-scale movements may regulate population density (e.g. WATERS 1965), facilitate mating and reproduction (LEHMANN 1967), enable (re)colonization or redistribution (HYNES 1970; TOWNSEND & HILDREW 1976; WILLIAMS & HYNES 1976), and may help to meet specific needs of certain taxa during various stages of the life cycle (DENNERT et al. 1969).

Colonization and/or redistribution are normally attributed either to downstream drift or upstream movements (see reviews of WATERS 1972; SÖDERSTRÖM 1987; STATZNER et al. 1984). Lateral movements or vertical movements upward from within the substrate can also contribute, as can large-scale movements such as mating and/or oviposition flights by adult insects. Downstream drift is usually considered to be the most important pathway for redistribution of lotic invertebrates (WATERS 1972; TOWNSEND & HILDREW 1976; WILLIAMS & HYNES 1976). Movement on the substrate surface or in the interstitium can contribute significantly to the redistribution of benthos (e.g. ELLIOTT 1971; BUTLER & HOBBS 1982; BENZIE 1984).

In order to quantify directional movements of lotic invertebrates various traps have been devised (STEINMANN 1913; WATERS 1965; MÜLLER 1966; LEHMANN 1967; HULTIN 1968; BISHOP & HYNES 1969; ELLIOTT 1971; OTTO 1971; TOWNSEND & HILDREW 1976). Two types of constructions are commonly used: traps that collect moving animals with nets, and colonization samplers, e.g. gravel-filled trays or cages that can be colonized by invertebrates from specific directions. Most of these samplers are limited, however, to either drift alone or to upstream movement alone, although there are exceptions (e.g. HOBBS & BUTLER 1981; PEARSON & JONES 1987; BERGEY & WARD 1989). These two main types of samplers have typical limitations: net-type traps tend to

clog with silt and drifting material (GOEDMAKERS & PINKSTER 1981; BUTLER & HOBBS 1982), limiting the duration of exposure to usually less than a few hours, in some cases to only a few minutes (DENNERT et al. 1969; BIRD & HYNES 1981). Hence, movements of animals with low moving activity are difficult to assess. Varying movement rates (MÜLLER 1974) as well as stochastic and/or local events can bias the results. Colonization samplers are placed either on the substrate surface or dug into the sediment. Samplers placed on the substrate surface are open predominantly for animals moving by drift and are unsuitable to record movements within the interstitium (WILLIAMS & HYNES 1976). Exposing and recovering buried substrates can cause considerable disturbance of the sampling area (BERGEY & WARD 1989) and induce escape reactions of the fauna (BRETSCHKO & KLEMENS 1986). Reproducibility is lowered further, because it is difficult to place buried substrates more than once in identical positions (PANEK 1991b).

A single sampling device that allows the assessment of movements in several directions and at the same time the clear discernment between surficial and interstitial movement is highly desirable, but rare. This paper describes a novel sampling device to assess the direction in which benthic invertebrates move within, on and above stream substrates and provides the results of a field test to illustrate its capabilities. The "Multidirectional Cage Trap" (further referred to as MDC-Trap) has nine modules and allows the measurement of up to nine different types of invertebrate movement simultaneously: upstream, downstream and lateral (left and right) movements at the substrate surface and within the subsurface sediments to a depth of 10 cm, and vertical movements upward from within the hyporheos. The trap was designed for use in streams with coarse sand, gravel or pebble substrates. It can be operated with minimal disturbance to the stream bed and enables repeated sampling of identical patches of stream bottom.

Study site

The study was carried out from 13 to 21 August, 1997 in the Ilm river, a nutrient-rich hardwater stream (stream order 4, Strahler classification) in Thuringia, Germany. The study site was located in the hyporhitric zone (50°55′9″ N, 11°19′20″ E; 255 m a.s.l.). The water slope was about 0.5% and stream width varied between 8 and 10 m. The substrate was mainly mixed gravel with sand and flat cobbles up to a maximum length of 20 cm embedded near the surface. The study site was partly shaded by a canopy of *Fraxinus excelsior*, *Acer campestre* and *Alnus glutinosa*. During the colder months the stretch is heavily colonized by diatoms and by the filamentous algae *Cladophora* sp. in the warmer months (SCHÖNBORN 1996).

A 70-year mean discharge of 4.2 $m^3 \cdot s^{-1}$ was recorded at a hydrograph station about 5 km downstream of the study site. Mean discharge during summer 1997 was 2.04 $m^3 \cdot s^{-1}$. During the study, average (± 1 S.D.) daily discharge was 1.69 (± 0.13) $m^3 \cdot s^{-1}$ and ranged from 1.54 to 1.71 $m^3 \cdot s^{-1}$ (unpublished data from Staatliches Umweltamt Erfurt). Between the study site and the hydrograph station there is only one sizeable tributary, contributing about 0.1–0.2 $m^3 \cdot s^{-1}$ (W. NERB, Institute of Geography, Friedrich-Schiller University Jena, pers. com.). Before and throughout the study no floods occurred and turbidity was low. Physical and chemical parameters showed little variation among the traps or during the experiment. Water velocity and depth were recorded at the beginning and the end of the colonization period above each MDC-Trap and taken to be the average of measurements at all four corners and at the centre of the trap. Current velocity was measured at 0.6× depth using an electromagnetic flowmeter. The depth varied from 0.21 to 0.24 m and current speed ranged from 0.48 to 0.82 $m \cdot s^{-1}$, with an average (± 1 S.D.) of 0.71 (± 0.14) $m \cdot s^{-1}$. Temperature, dissolved oxygen, electrolytical conductivity and acidity were measured daily during the experiment using portable digital instruments. Water temperature ranged from 15.8 to 16.4 °C, conductivity averaged (± 1 S.D.) 690 (± 66) $\mu S \cdot cm^{-1}$, pH = 8.33 (± 0.04) and oxygen = 13.1 (± 0.8) $mg \cdot l^{-1}$.

Materials and Methods

Multidirectional Cage Trap

The MDC-Traps were made of waterproof 9 mm plywood frames that were divided into nine compartments each (Fig. 1A). All plywood components, the outer and inner walls of the frame as well as the base, were perforated with series of holes of 10 and 18 mm to allow invertebrates easy access. The nine compartments were loaded with identical directional cages that were open for colonization from one side only (Fig. 1B). The cages were made of gravel filled wire-mesh baskets (1.05 cm mesh) and could be rotated in any direction and be placed in any compartment. Depending on the direction into which the open side was positioned, only animals arriving from this direction could enter the cage. Five of the six sides of each cage were lined with a screen of fine gauze (0.100 mm mesh) which prevented macroinvertebrates from entering the cage. It was assumed that flow conditions within the trap were largely similar to adjacent natural sediment and that the lining had little impact on interstitial flow of water.

In order to optimize the selectivity for recording movements on the sediment surface, a construction of plexiglass baffles was placed on top of the plywood frames (Fig. 1C). Vertical pieces fixed parallel to the current prevented surficial lateral access, tilted pieces prevented surficial access by drift or by upstream movement.

The directional cages were filled with dried gravel that had been purchased close to the study area. The fill mixture consisted of the same mineral components as the natural sediment and provided a heterogenous substrate with interstitial spaces similar to the natural substrate. The filling was mixed of 40% gravel with a mean diameter of 24 mm (range 16–32 mm) and 60% gravel with a mean diameter of 12 mm (range 8–16 mm). Grain sizes smaller than 8 mm were not

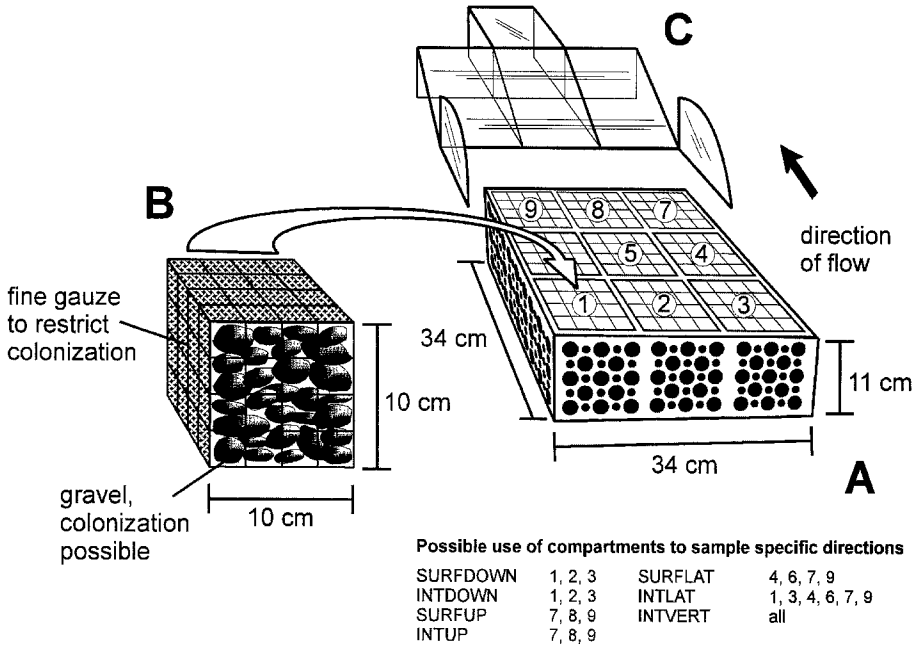

Fig. 1. Design of the Multidirectional Cage Trap (MDC-Trap). **(A)** Perforated plywood frame with compartments, **(B)** directional cage prepared with a screen of fine gauze and filled with gravel, **(C)** plexiglass baffles, ①–⑨ compartment number. For abbreviations see Table 1.

used. At the beginning of the experiment there was no *aufwuchs* present. The frames together with the directional cages were buried into the stream with the upper edges flush to the sediment surface. The MDC-Traps proved to be very resistant to dislocation even during high flow conditions and no further fixation was needed to securely anchor the traps.

Experimental Design

A set of three MDC-Traps (A, B and C) was placed in a row in the middle of the Ilm river. The compartments of each trap were numbered consecutively from 1 to 9, beginning at the orographically left upstream corner. The number of cages oriented in the same direction differed among the traps. This allowed greater numbers of replicates for measuring certain movement modes (Table 1). The distance between every MDC-Trap was 1 m, the distance from the outer traps to the banks was about 3 m. Ambient conditions, in particular the nature of the stream bed and current, were considered to be homogenous for all three traps. Because an undisturbed benthic assemblage was to be assessed, the traps were buried six weeks prior to the experiment to allow the neighbouring benthic community to recover from the disturbance caused by the initial burying. During the pre-experimental period, the compartments were loaded with "dummy-cages" to keep them free of sediment. At the beginning of the measurement period the dummy-cages were replaced by directional cages.

Based on earlier experiments with gravel filled wire-mesh baskets in the Ilm river (ELSER 1999), the directional cages were allowed to colonize for 8 days. At the end of this period the cages were taken out beginning with the downstream compartments. During the removal a V-shaped wooden baffle was placed directly upstream of each trap to reduce the current. As soon as the cages were lifted slightly, a plexiglass piece (12 × 12 cm) was held against the open side of the directional cage to minimize animal wash-off. In preliminary experiments a net was placed downstream also to capture washed off animals, but this technique lead to overestimations of invertebrate numbers because organisms clinging to the outer surface of the cages were also washed into the net.

After removing a directional cage, the empty compartment was reloaded immediately with a new cage in order to avoid animal wash-off from neighbouring compartments due to suddenly changing flow conditions. Recovered cages were placed into separate plastic buckets with the open side facing upwards. The outsides were

Table 1. Loading of the Multidirectional Cage Traps with directional cages with abbreviations for movement modes and number of replicates per type of invertebrate movement. Lateral movements directionally towards and from the banks have been pooled since the samples did not differ substantially.

Mode of movement/ type of directional cage	Abbreviation	Trap A [replicates]	Trap B [replicates]	Trap C [replicates]	Σ (n =)
Surficial downstream	SURFDOWN	2	2	1	5
Interstitial downstream	INTDOWN	1	1	2	4
Surficial upstream	SURFUP	1	1	1	3
Interstitial upstream	INTUP	1	2	1	4
Surficial lateral	SURFLAT	1	1	1	3
Interstitial lateral	INTLAT	2	1	2	5
Vertically upward from within the substrate	INTVERT	1	1	1	3

brushed thouroughly to remove adhering animals. Afterwards, the cages were opened and the whole content was washed into a plastic bag with 70% ethanol. In the laboratory the cage contents were rinsed through a sieve (0.250 mm mesh). All invertebrates were counted and identified to the lowest possible taxonomic level using a dissecting microscope.

In order to allow comparisons with the natural benthic assemblage, five benthic samples were collected at the end of the experiment using a modified Hess-sampler (sampled area 0.043 m^2, 0.250 mm mesh). A marked srewdriver was used to fix a sampling depth of 10 cm, which corresponded to the height of the directional cages. Samples were taken in the same stretch of stream at sites similar to those where the MDC-Traps were buried. Samples were processed as described above.

Data analysis

As a measure of similarity, an agglomerative cluster analysis was carried out on the dominance structure (relative dominance) of the animal assemblages in the directional cages and in the benthic samples. Afterwards, counting data were $\log_{10}(x+1)$ transformed to stabilize variances. Normal distribution of data was checked by conducting Kolmogorov-Smirnov-tests. Principal Component Analysis (PCA), as provided by software package CANOCO (TER BRAAK 1987), was used to detect differences and similarities between animal assemblages among the directional cages. PCA is a variance oriented ordination technique suitable for identifying differences between data sets. PCA-plots show relationships among the directional cages, among the different taxa, and also between the taxa and the cage types. The aim of PCA is to set up a secondary coordinate system amongst the scatter of data points with the maximum increase of variance along axis I. The algorithm for PCA-axis II, which is orthogonal to axis I, and further axes is analogous. PCA-axis I represents the greatest increase of variance within the data set. Data points appearing more distant from the axis origin represent a high proportion of total variance whereas points close to the origin contribute less to overall variance. Eigenvalues indicate the proportion of variance represented by each PCA-axis. Consequently, mean numbers of common taxa were compared by one-way ANOVA that was followed by Tukey's HSD-tests for multiple comparisons among means (MOTULSKY & SEARLE 1998).

Results

After the 8-d colonization period, a total of 24 macroinvertebrate taxa was collected in the MDC-Traps with an average (± 1 S.D.) of 9.8 (± 2.36) taxa per trap (Table 2). The assemblages were dominated both taxonomically and numerically by insects. An average (± 1 S.D.) of 3985 (± 194) individuals was caught in each MDC-Trap. Chironomids dominated by far, representing 76.3% of the total catch whereas their relative abundance in benthic samples was lower. Caddis larvae and mayflies were less dominant, both in benthos and MDC samples. Non-insect invertebrates included mainly crus-

Table 2. Numbers of individuals and relative abundances of common taxa in MDC-samples (sum of all 27 directional cages) and in benthic samples (means ± 1 S.D.). MDC-catches were scaled up to 1 m^2 to allow comparisons to the natural benthic assemblage. Taxa that contributed less than 0.1% to benthic and MDC-samples are listed as "others".

		Sum of all MDC-Traps		Natural benthos	
		[Indiv. · m^{-2}]	[%]	[Indiv. · m^{-2}]	[%]
Tricladida	*Dugesia gonocephala* (DUGES)	4	0.01	74 ± 44	0.18
Pulmonata	*Ancylus fluviatilis* MÜLLER	63	0.14	1516 ± 603	3.67
Hirudinea	*Erpobdella octoculata* L.	181	0.39	170 ± 112	0.41
Ostracoda		26	0.06	147 ± 154	0.36
Copepoda	*Eucyclops serrulatus* FISCHER	837	1.79	488 ± 200	1.18
Isopoda	*Asellus aquaticus* L.	281	0.60	18 ± 30	0.04
Amphipoda	*Gammarus pulex* L.	1189	2.55	3014 ± 1007	7.30
Hydracarina	Hydrachnellae	48	0.10	396 ± 303	0.96
Ephemeroptera	*Baetis rhodani* PICT.	2444	5.24	5594 ± 3174	13.55
	Serratella ignita PODA	78	0.17	424 ± 90	1.03
Plecoptera	*Leuctra* sp. STEVENS	44	0.10	–	–
Coleoptera	*Elmis* sp.	7	0.02	336 ± 205	0.81
Trichoptera	*Rhyacophila nubila* ZETT.	181	0.39	1567 ± 344	3.80
	Hydroptila spp. DALMAN	163	0.35	682 ± 150	1.65
	Hydropsyche spp. PICTET	5330	11.42	6271 ± 4218	15.19
	Sericostoma personatum K. & SP.	30	0.06	258 ± 233	0.63
Diptera	Chironomidae	35596	76.33	19211 ± 6371	46.53
	Simuliidae	93	0.20	267 ± 115	0.65
	Dicranota sp.	7	0.02	484 ± 247	1.17
	Bezzia sp.			111 ± 117	0.27
Others		67	0.09	143 ± 115	0.35

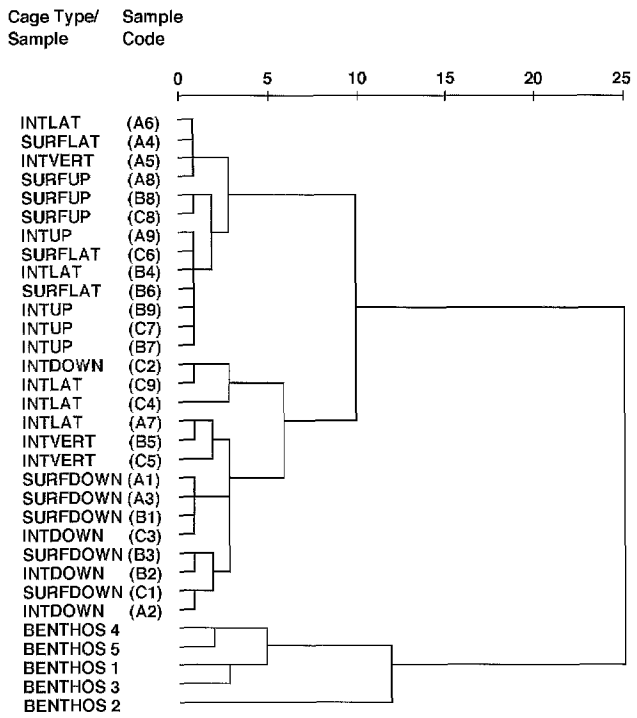

Fig. 2. Similarity of invertebrate assemblages (relative dominance of all taxa) in the directional samples and in the benthic samples presented as dendrogram using average linkage between groups (squared Euclidean distance). The sample code identifies the location of a sample in trap A, B and C and the number of the compartment from 1–9. For abbreviations see Table 1.

taceans such as *Gammarus pulex*, *Eucyclops serrulatus* and *Asellus aquaticus*. With the exception of a few rare specimens of dipteran larvae, water beetles and mussels, all other taxa collected in benthic samples also occurred in the MDC-Traps. Taxa recorded only in the MDC-Traps were restricted to few plecopteran larvae. Compared to benthic samples, a marked under-representation of *Ancylus fluviatilis*, *Gammarus pulex*, Ephemeroptera, most Trichoptera and *Dicranota* was recorded in the MDC-Traps, while *Eucyclops serrulatus* and *Asellus aquaticus* were over-represented.

Cluster analysis showed that the samples formed three major groups (Fig. 2). One group contained all benthic samples, indicating that dominance structure in the directional cages and the natural benthic assemblage differed strongly. The second group contained all downstream samples (SURFDOWN, INTDOWN), three of five INTLAT samples and two of three INTVERT samples. The third group included all upstream samples (INTUP, SURFUP), all SURFLAT samples and the remaining INTLAT and INTVERT samples.

PCA showed that samples separated along a gradient with SURFUP at one end of PCA-axis I and SURFDOWN at the opposite end of the axis (Fig. 3A). The SURFDOWN, INTDOWN and SURFLAT samples formed relatively tight groups by themselves, indicating great similarities within the sample group. Between INTLAT, INTVERT and INTDOWN, however, lower similarities emerged within the groups. This rating was confirmed by the distribution along PCA-axis I vs. III (Fig. 3B) which showed a similar pattern.

Depending on their pattern of directional movement, common taxa were categorized into three groups. Taxa belonging

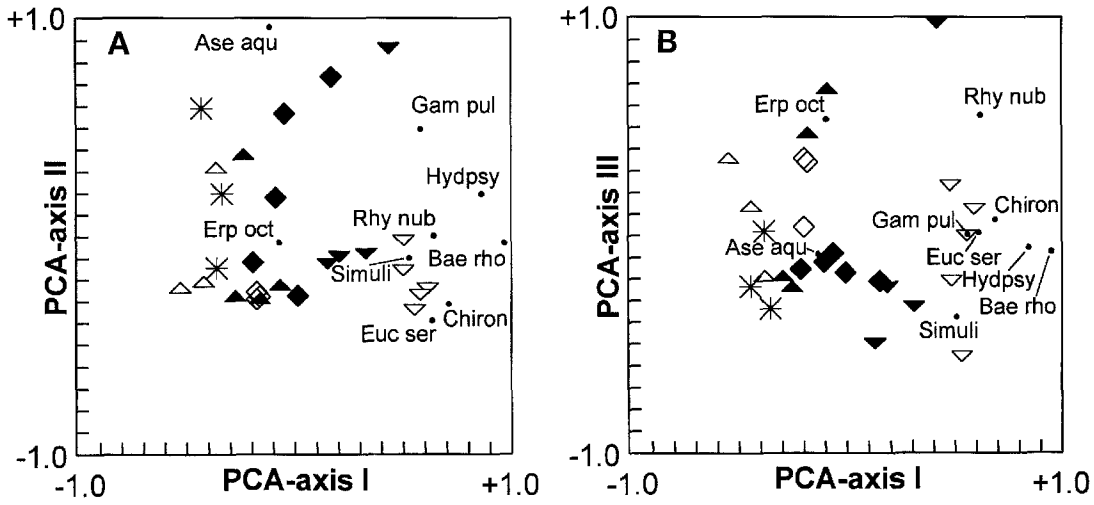

Fig. 3. Species-sites PCA-plots (eigenvalues 0.42/0.15/0.12/0.06). **(A)** PCA axes I vs. II, **(B)** PCA axes I vs. III. Abbreviations: **Ase aqu** *Asellus aquaticus*, **Bae rho** *Baetis rhodani*, **Chiron** Chironomidae, **Euc ser** *Eucyclops serrulatus*, **Erp oct** *Erpobdella octoculata*, **Gam pul** *Gammarus pulex*, **Hydpsy** *Hydropsyche* spp., **Rhy nub** *Rhyacophila nubila*, **Simuli** Simuliidae. Types of directional cage (for abbreviations see Table 1): △ SURFUP, ▽ SURFDOWN, ◇ SURFLAT, ▲ INTUP, ▼ INTDOWN, ◆ INTLAT, ✳ INTVERT.

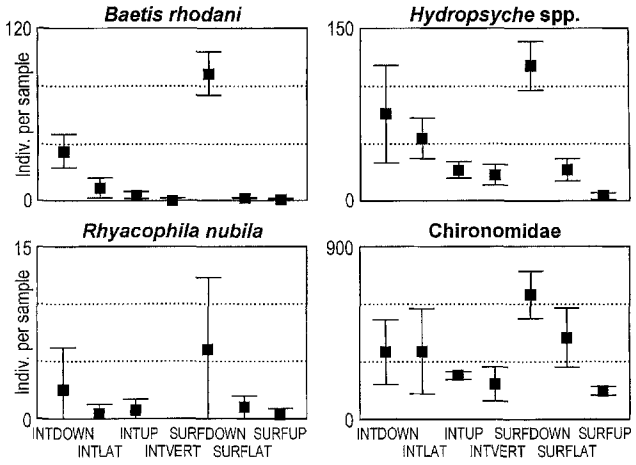

Fig. 4. Distribution of *Baetis rhodani*, *Hydropsyche* spp., *Rhyacophila nubila* and Chironomidae on different types of directional cages (mean numbers of individuals ± 1 S.D.). For abbreviations see Table 1.

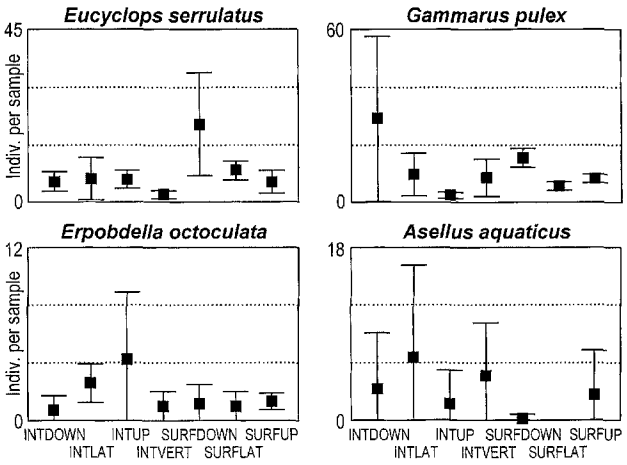

Fig. 5. Distribution of *Eucyclops serrulatus*, *Gammarus pulex*, *Erpobdella octoculata* and *Asellus aquaticus* on different types of directional cages (mean numbers of individuals ± 1 S.D.). For abbreviations see Table 1.

Table 3. Comparison of the distribution of dominant invertebrate taxa on types of directional cages as indicated by Tukey's HSD-test for multiple comparisons (* = $P < 0.05$, ns = not significant). For abbreviations see Table 1.

Modes of movement/ types of directional cages			*Baetis rhodani*	*Hydropsyche* spp.	Chironomidae	*Gammarus pulex*	*Eucyclops serrulatus*
SURFDOWN	vs.	INTDOWN	*	ns	ns	ns	ns
SURFDOWN	vs.	SURFUP	*	*	*	ns	ns
SURFDOWN	vs.	INTUP	*	*	*	*	ns
SURFDOWN	vs.	INTLAT	*	ns	ns	ns	*
SURFDOWN	vs.	SURFLAT	*	*	ns	ns	ns
SURFDOWN	vs.	INTVERT	*	*	*	ns	*
INTDOWN	vs.	INTUP	*	ns	ns	*	ns
INTDOWN	vs.	SURFUP	*	*	ns	ns	ns
INTDOWN	vs.	SURFLAT	*	ns	ns	ns	ns
INTDOWN	vs.	INTLAT	*	ns	ns	ns	ns
INTDOWN	vs.	INTVERT	*	*	ns	ns	ns
SURFUP	vs.	INTUP	ns	*	ns	ns	ns
SURFUP	vs.	INTVERT	ns	*	ns	ns	ns
SURFUP	vs.	SURFLAT	ns	*	ns	ns	ns
INTLAT	vs.	SURFUP	*	*	ns	ns	ns
INTLAT	vs.	INTVERT	*	ns	ns	ns	ns

the first group exhibited a clear preference for downstream movement by drifting or crawling and seldom displayed upstream or lateral movement. In particular, *Baetis rhodani* and *Hydropsyche* spp. showed highest abundances in SURFDOWN-cages followed by INTDOWN (Fig. 4). Both taxa discriminated clearly between surficial downstream and other directional movements, and mean numbers in SURFDOWN-cages and other cage types differed significantly in nearly all cases (Table 3). *Rhyacophila nubila* was also assigned to this group, although data were non-normally distributed and ANOVA could not be carried out. Preference for downstream movement was less pronounced in the second group which included chironomids and *Eucyclops serrulatus*. Abundance of chironomids and *E. serrulatus* was highest in SURFDOWN-cages, however, results were significant only in few cases. Note that data for Chironomidae include several species, each of which may have a different movement pattern. In contrast to surficial movements, no directional preferences were detected within the interstitium for both taxa. Taxa belonging to the third group either exhibited only slight directional preferences or were about equally distributed among all cage types. E.g. *Gammarus pulex* preferred INTDOWN to SURFDOWN cages and SURFDOWN to INTUP while *Erpobdella octoculata* did not discriminate between any moving direction (Fig. 5). Taxa such as *Asellus aquaticus*, *Ancylus fluviatilis* and *Hydroptila* spp. were also assigned to the group, however, counts were low and do not permit further conclusions.

Movements vertically up from within the hyporheos were infrequent. *B. rhodani* and *R. nubila* exhibited almost no vertical movement at all, whereas the crustaceans *G. pulex*, *E. serrulatus* and *Asellus aquaticus*, as well as *Hydropsyche* spp. and chironomids moved vertically to some degree.

Discussion

The study demonstrated the complex nature of benthic invertebrate movement. TOWNSEND & HILDREW (1976) suggested that the stream benthos is continually redistributed through drift and recolonization, and SHELDON (1977) proposed that the fauna of each section of a stream is in a transitory equilibrium maintained by high rates of immigration and emigration. Transitory occupation of adjacent habitat units by diffusion-like movements is probably an integral part of the life history tactics of many taxa (PAJUNEN 1977). Certain species may migrate in different manners and in different directions throughout their lives (see DENNERT et al. 1969).

Whereas invertebrate drift has been the object of considerable study (see reviews by WATERS 1972; STATZNER et al. 1984), upstream movement has received less attention (SÖDERSTRÖM 1987). Studies involving benthic movement in directions other than up- or downstream are even more infrequent (but see PANEK 1991a, b; BENSON & PEARSON 1987; BERGEY & WARD 1989; PEARSON & JONES 1987). There is, however, a pressing need to incorporate such processes into models of population and community phenomena in streams. One likely factor for the paucity of research in this field is the difficulty in sampling directional movement in the benthos as compared with that of the water column. The MDC-Trap has been designed to help close this gap and results of first field tests are promising.

The main advantage of the MDC-Trap is its potential to discriminate simultaneously among several directions and modes of benthic invertebrate movements. The device is easily operated and allows determination of whether movement occurs at the surface or interstitially. Sampling of the same spot of substratum can be done repeatedly without causing disturbance to the stream bed. Due to the construction there is no clogging and, once exposed, the device can be left in the stream indefinitely. The first set of MDC-Traps reported here was exposed in July 1997 and has not been recovered before October 1999. During that period none of the traps was severely damaged or lost. Nevertheless, the device could also be employed in short-term studies, e.g. to assess day-night periodicity of invertebrate movement. In contrast to net-type traps, e.g. those of BUTLER & HOBBS (1982), GOEDMAKERS & PINKSTER (1981) or HULTIN et al. (1969), the direction-sensitive subunits are easily accessible to animals. Likewise, specimens wandering into the directional cages can also move out if conditions do not meet their specific needs. Hence, retrieved directional cages are likely to contain numbers and varieties of animals that reflect the natural benthic colonization activity of the preceding exposure period. By varying the exposure time the device can be used to determine relative activity levels of selected taxa.

Inevitably, there are limitations to the technique, but these seem minor in comparison to the advantages. Some bias could be due to animals entering the cages from directions other than the assessed ones. Although the directional cages fitted quite closely to the plywood compartments, organisms may have crawled along the gauze screens until they found an entrance. In effect, the spaces between the cages and the frame could have provided a series of channels by which invertebrates could have moved freely in any direction.

Smaller organisms could have even passed through the screens. For chironomids there is evidence that larvae are attracted by gauze screens and quasi colonize gauze by using the mesh pores as templates for their tubes (BISHOP & HYNES 1969). On the other hand, some animals possibly refrained from entering as has been described for some upstream-movement traps (HULTIN et al. 1969). Furthermore, baffles, particularly those transverse to the flow, may have changed physical conditions in or over the compartments and may have influenced movement to or from cages. However, this is a common failing of many upstream movement traps (see e.g. HOBBS & BUTLER 1981).

Obviously, not all potential colonizers invaded the directional traps with equal success and some taxa were trapped in low numbers even though these species were abundant in benthic samples. Possibly, the spaces between the cages acted as a sink for animals that otherwise would have entered a cage. It is widely accepted, though, that benthic invertebrates colonize at different rates depending on their specific mode of movement and on their propensity to move (e.g. TURCOTTE & HARPER 1982; KOHLER 1983; ALLAN 1984). The feature of differential "activity rates", or "mobility indices" has been discussed by several authors (LANCASTER et al. 1990; PANEK 1992; PEARSON & JONES 1987; WINTERBOTTOM et al. 1997). However, quantitative estimates are available only for a few taxa. Here, comparisons among studies can be made only for chironomids and for *Baetis rhodani*. Above the sediment and within the water column chironomids are highly mobile (HILDREW & TOWNSEND 1976; LANCASTER et al. 1990) with a mobility index increasing with the mean daily discharge. WINTERBOTTOM et al. (1997) assumed that chironomid mobility in Broadstone Stream (southern England) is mainly driven by the influence of flow on drift. On the other hand, PANEK (1991a, b) found comparably low activity for chironomids when investigating invertebrate movements inside the bed sediments of a prealpine brook (Seebach, Austria). In support of WINTERBOTTOM et al. (1997), chironomid densities were always highest in SURFDOWN-cages and chironomids appeared to be highly mobile drifters. At the same time there was a remarkable proportion of specimens showing downstream or lateral movement inside the sediment, indicating that subsurface mobility of chironomids was substantially higher than PANEK (1991a) found in the Seebach. Note that the above mentioned studies were restricted either to surficial or to interstitial movement only.

Various species of *Baetis* are often cited as having a high degree of mobility, too (HYNES 1970; WATERS 1972), and the feature of downstream drifting baetids has been widely described (e.g. BOHLE 1978; PLOSKEY & BROWN 1980; BIRD & HYNES 1981; CAMPBELL 1985; STATZNER & MOGEL 1985).

However, baetids are also reported to move upstream (ELLIOTT 1971; BROWN & BROWN 1984) and HULTIN et al. (1969) recorded *Baetis rhodani* moving extensively upstream shortly before emergence. KOHLER (1983) reported random movements on and within the substrate for the same genus. In support of most drift studies, *Baetis rhodani* were caught in SURFDOWN-cages with great prevalence and to a much lesser degree in INTDOWN-cages, indicating that drift was the most important mode of movement for this species. Directions other than downstream were not significant. This is consistent with the findings of LAVANDIER (1982, 1991) who hypothesized that population stability of *Baetis* is maintained by the flight of reproductive females upstream or by young larvae which are numerous within the substratum.

If less active taxa are to be assessed, an exposure time longer than eight days seems advantageous. However, varying the duration of exposure time can alter the findings (COVER & HARREL 1978; ELSER 1999). When working with upstream-movement nets, e.g. GOEDMAKERS & PINKSTER (1981) found that the number of animals trapped in 24 hours was up to seven times as large when the nets were emptied every hour instead of once every 24 hours. Several workers investigating the colonization dynamics of lotic invertebrates have noted that artificial as well as natural substrates are modified when placed in streams (SHELDON 1977; MINSHALL & MINSHALL 1977; ULFSTRAND et al. 1974). Changing food availability, increasing predation or density dependent responses like inter- and intraspecific competition can lead to changes in community structure (LANCASTER et al. 1990; PECKARSKY 1985). In general, the calculations of invertebrate colonization activity are sensitive to the exposure time, the natural abundance of a taxon and the rates of movement of other taxa. Further, the colonization activity relies on the substratum in the traps being equally attractive to all taxa, and on relative attractiveness remaining constant during exposure. This variability has not been quantified in the present study and therefore it remains unclear whether the apparent differences should be regarded as significant. To further investigate this topic, it would be desirable to compare different exposure times of directional cages. Additionally, in order to evaluate possible position effects (SÖDERSTRÖM 1987) MDC-Traps should be placed both near the banks and in the mid-channel.

While some investigators have found substrate-associated movement always to be random (HART & RESH 1980; BIRD & HYNES 1981; BENSON & PEARSON 1987), NIELSEN (1950) postulated that rheotactic orientation of insects (positive thigmotaxis) would cause all "random movements" to be against the current, even in the hyporheos. Despite the lack of a definite current, movements should always be upstream because animals would orientate themselves to the slight flow that delivers oxygen and food particles (BISHOP & HYNES 1969). My findings are in contrast to both assumptions. Insects neither moved randomly nor predominantly against the current. Longitudinal movement was in the downstream direction for most insects, although the taxon-specific patterns varied considerably. As indicated by multivariate analyses, taxa arranged along a gradient beginning with the SURFDOWN-cages and ending with SURFUP. Net downstream displacement, both on the substrate surface and inside the sediment, was evident for most taxa. Certainly, to some degree this pattern simply reflected the type of microhabitat where the animals dwell: e.g. *Baetis* larvae mainly inhabit the top 10 cm of the stream bed, especially larvae in early instars (LAVANDIER 1991), and are infrequent in deeper sediment layers (PANEK 1991a). Nevertheless, the distinct upstream-downstream disparity suggests a non-random component of aquatic insect movement, even in the interstitial zone where positive thigmotaxis is less pronounced. Possibly, *Baetis* and *Hydropsyche* moved downstream by using the water current as a vehicle for redistribution (see reviews of WATERS 1972; SÖDERSTRÖM 1987; STATZNER et al. 1984). Although energetics have not been measured explicitly, I assume that insects preferred less energy consuming types of movement whereas the more energetic pathways like upstream movement on the sediment surface were avoided.

Even homotopic non-insects were poor upstream movers. In contrast to MEIJERING (1972), *Gammarus pulex* and *Asellus aquaticus* showed about equal propensities to move upstream, downstream and laterally in the interstitium. Compared to insects, surficial downstream movement of both species was substantially lower, though. This is consistent with LIGHT & ADLER (1983) who suggested that invertebrates lacking a flying stage in the life cycle will have relatively less downstream displacement, either less drift or greater upstream movement.

The effect of upstream movement as a compensatory mechanism for downstream displacement has been discussed in several papers (e.g. MINCKLEY 1964; BISHOP & HYNES 1969; ELLIOTT 1971; MEIJERING 1972; WILLIAMS & HYNES 1976), but it is still uncertain whether the aim is to compensate drift or if it is merely a behavioural response of the individual in relation to changing biotic or abiotic conditions (SÖDERSTRÖM 1987). A good deal of local mobility can probably be attributed to accidential transport events driven by the physics of the habitat (LANCASTER et al. 1996). The only taxon that compensated downstream displacement to a perceptible degree by interstitial upstream movement was *Erpobdella octoculata*, but absolute numbers were too low to permit a detailed interpretation. As a whole, the results obtained with the MDC-Trap suggest that it might be reasonable to put the idea of quantitative drift compensation by upstream migrations (*sensu* MÜLLER 1974) in question. Possibly, upstream movement does not represent a serious counter mechanism to the much greater downstream drift. Note, however, that above mentioned compensation figures do not take into account the distances travelled in drift or upstream movement.

The hyporheos may act as a flow refugium to invertebrates during high discharge (PALMER et al. 1992; PALMER et al.

1995; LANCASTER & HILDREW 1993; DOLE-OLIVIER et al. 1997) or may hold a seed bank (ZWICK 1996) which facilitates recolonization of denuded areas after disturbance. In support, my experiment showed that many taxa exhibited vertical movements upwards. Exceptions were *Baetis rhodani* and *Rhyacophila nubila*. The most active vertical movers were *Hydrospyche* spp., Chironomidae, *Gammarus pulex* and *Eucyclops serrulatus*. However, the absolute numbers of animals captured with INTVERT-cages remained low. Probably, this was due to the fact that the experiment was carried out in a phase of stable discharge where there was no need or no possibility for specimens dwelling in deeper sediment layers to move to the substrate surface. Furthermore, it has to be considered that results refer to a single experiment conducted in summer and did not take into account possible seasonal differences. It would be desirable to carry out similar investigations in different seasons as well as immediately after bedload transporting spates to evaluate further the pathways of benthic invertebrate redistribution and/or recolonization.

Acknowledgements: I would like to express my thanks to SONJA HORNUNG, SUSANNE KORZUCH and FRANZ WAGNER for their inspiration and many helpful discussions. Thanks go to WILFRIED SCHÖNBORN for advice during the study. SUSANNE KORZUCH and WOLFGANG SCHMALZ assisted in the field work. JÖRG PERNER helped performing the multivariate analyses. I greatly appreciate the suggestions and comments of JILL LANCASTER (Edinburgh) on an earlier draft of this paper. The study was supported by grants from the Deutsche Forschungsgemeinschaft (Förderkennzeichen GRK 266/1-96).

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Received: January 17, 2000
Accepted: May 18, 2000

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